THE BURROW OF THE GOPHER TORTOISE

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Fronted by its asymmetric apron of subsoil, the cavernous entrance and burrow of the eastern gopher tortoise, *Gopherus polyphemus* (Daudin), has long intrigued naturalists and herpetologists. Auffenberg (1962) postulates that the burrowing habit of the genus *Gopherus* has evolved as an effective manner in escaping subthreshold surface temperatures and is practiced only in areas where winters are sufficiently cold to warrant this type of activity. The literature indicates that the eastern form is the only North American species that consistently digs a long permanent burrow. Relatively little study has been given to the subterranean abode of this chelonian species other than the early work by Hallinan (1923). Hallinan studied 19 burrows in the Lakeland soil series of Duval County in northern Florida.

The present work is a comparative analysis of the burrow systems in three different soil types, Lakeland, Lakewood, and St. Lucie soils. The Lakeland and St. Lucie soil sites studied were located near DeLand, Volusia County, Florida. The Lakewood soil habitat was studied near Silver Glen Springs in the Ocala National Forest, Lake County, Florida. The Lakeland sand supports a plant association dominated by the longleaf pine (*Pinus australis*) and turkey oak (*Quercus laevis*) and is classified as a well drained non-calcareous sand (Bryan, 1960). Both the Lakewood and St. Lucie sands support a plant association of sand pine (*Pinus clausa*) and scrub oaks (*Q. chapmani, Q. myrtifolia, Q. virginiana geminata*) and belong to the excessively drained non-calcareous sands of Florida.

For the manual excavation of 13 burrows, appreciation is here expressed to my students of natural history and ecology. Thanks are also given to Dr. Warren F. Jones, Jr., of Stetson University for his assistance with some of the statistical problems of the study.

Materials and Methods

Measurements of 13 excavated burrows (length, vertical depth, angle of declination, and burrow diameter) and their tortoise inhabitants (greatest carapace length, width, and depth) are recorded in Table 1. The tortoises were measured with large wooden cali-

TABLE 1

Gopher tortoise and excavated burrow measurements

No.	Sex	Carapace Length in mm.	Greatest Width in mm.	Greatest Depth in mm.	Burrow Length in inch.	Burrow Depth in inch.	Angle of Decline degree	Entrance Width in inch.	Entrance Depth in inch.	Width at 2 ft. in inch.	Depth at 2 ft. in inch.	Soil Type*
1	F	146	111	62	114	55	30	7.8	4.3	5.3	3.0	L
2	F	159	122	67	178	70	24	8.0	3.8	7.0	3.5	L
3	F	179	139	75	168	63	23	7.8	4.0	7.0	3.3	L
4	M	196	152	86	198	104	32	8.5	4.0	7.0	3.3	L
5	F	177	134	76	139	71	31	7.8	4.0	6.3	3.3	L
6	F	277	218	120	242	67	17	12.5	5.5	9.5	5.5	L
7	F	162	122	70	126	65	31	7.5	3.5	6.0	3.0	L
7†	(F)	(162)	(122)	(70)	106	68	39	(7.5)	(3.5)	6.3	3.3	(L)
8	F	149	113	59	152	70	28	6.0	2.5	5.8	2.5	Lw
9	M	227	167	98	180	110	38	10.0	5.0	8.0	4.3	Lw
10	M	217	161	90	188	92	30	12.0	6.5	9.0	5.0	Lw
11	F	174	127	67	161	77	29	9.3	4.3	7.8	4.0	SL
12	M	181	136	73	168	75	27	8.0	3.8	6.8	3.3	SL
13	F	145	113	62	166	78	28	7.3	3.3	6.5	3.3	SL

* Soil type: L, Lakeland; Lw, Lakewood; SL, St. Lucie.
† Double burrow.

pers to the nearest millimeter. Thirty-eight additional burrows were measured for length using a heavy plastic garden hose. To facilitate the passage of the hose down the burrow, a furniture caster with a two-inch wheel was secured to the end of the hose (Allen, 1961). Usually, the wheel could be heard as it struck the shell of the tortoise. For all 51 burrows, measurements were taken of the exposed subsoil fronting the burrow entrance, the height and width of the burrow entrance, and a second similar measurement two feet down the burrow. A compass reading was taken to determine the direction of the burrow entrance. Notes were recorded on the type, location, and abundance of vegetation near the burrow entrance.

RESULTS

Burrow Length. A wide range of burrow-length measurements for *Gopherus polyphemus* are found in the literature; 10-35 feet (Carr, 1952), 10.5-20 feet (Hallinan, 1923), 12-18 feet (Hubbard, 1893), 10-20 feet (Oliver, 1955), with a maximal length of 35-40 feet (Young and Goff, 1939). Measurements of 51 burrows in the present study varied from a minimum length of 6.3 feet to a maximum of 47.5 feet, with a mean length of 15.3 feet. Hallinan (1923) reported an average of 14.5 feet for 19 burrows.

After a number of burrows had been measured, it seemed apparent that burrows having larger diameter dimensions also had greater lengths. A coefficient of correlation calculated for 51 measurements of burrow width against burrow length resulted in a strong positive correlation ($r = .72$, $P < 0.01$). A comparison between 51 measurements of burrow height to burrow length also gave a significant correlation ($r = 64$, $P < 0.01$).

Hallinan (1923) postulated that the length of a burrow is determined by the moisture content of the soil. If this hypothesis were valid, it would seem that burrows might be longer in the better drained Lakewood and St. Lucie soils than those in the less well-drained Lakeland soil. Since it had been found that burrow diameter was correlated to burrow length, it was necessary to determine whether the three populations were of an equivalent size range. A t test between burrow-width measurements from the Lakewood soil (19 burrows) and the Lakeland soil (23 burrows) resulted in a significant difference ($t = 3.42$, P. < 0.01). A comparison between the Lakewood and St. Lucie soil (9 burrows) was also significant (t = 3.85, $P < 0.01$). The difference between burrow widths for the Lakeland and St. Lucie lacked significance (t = 1.4, $P > 0.05$). Thus, with disproportionate populations it became necessary to use a statistic which would hold the burrow diameter constant. A two matched-group design t test was used for this particular case. Eight pairs of comparable-sized burrows from the Lakeland and St. Lucie soils failed to show a significant difference in burrow length (t = 1.73, $P > 0.05$). Similarly, comparisons between 8 pairs of burrows in the Lakeland and Lakewood soils, and 7 pairs from the Lakewood and St. Lucie, lacked significance (t = 1.34, $P > 0.05$; t = 1.30, $P > 0.05$, respectively.

As a second check on these data, the analysis of variance was used to test for possible significant variations between burrow width/length ratios for the three habitats. This statistic resulted in a lack of significance at the 5 per cent level of confidence ($F = 1.38$, $P > 0.05$), implying no variation in the width/length ratios.

Although individual variations differ widely in the burrows of the three habitats, the above comparisons (two matched-group t test and analysis of variance) would indicate that no significant difference exists in burrow lengths for the three soil types.

Size of the gopher tortoise was correlated with burrow length. Measurements from 13 specimens (greatest width and greatest depth) correlated strongly with the burrow length ($r = .84$, $P < 0.01$; $r = .79$, $P < 0.01$, respectively).

Vertical Depth of Burrows. Young and Goff (1939) state that "the vertical distance from the surface to the end of the burrow appears to be determined by the resistance of the underlying material or by the water table". These writers report vertical depths ranging from 3-8 feet depending upon the underlying parent materials. In the present study, vertical depth measurements for 14 excavated burrows varied from 4.6 to 9.2 feet, with a mean of 6.5 feet. Although the burrows of the Lakewood soil had a greater average depth (91 inches) than those of the St. Lucie (76 inches) or Lakeland (70 inches), a t test analysis failed to show that the three populations differed significantly.

Measurements for the 14 excavated burrows failed to show a significant correlation between burrow length and vertical depth ($r = .43$, $P > 0.05$). This lack of correlation is probably explained by the wide variation in declination angles from this sample. Although burrow width and height were correlated with burrow length, neither of these diameter measurements were significantly correlated with vertical depth ($r = .34$, $P > 0.05$; $r = .40$, $P > 0.05$, respectively). Based upon burrow length, or from burrow diameter measurements, it was hoped that a predictive value could be given to estimate the vertical depth. However, from the low correlation between these measures and vertical depth, it was impossible to give a reliable value for such a prediction.

Declination Angle of Burrows. The mean angle of declination for 14 burrows was in remarkable agreement with that of Hallinan (1923). Twelve declination angles from Hallinan averaged 27° with the extremes between 15-45°. In this work the mean angle of declination was 29° with a range of 17-39°.

Horizontal Direction of Burrows. In considering the horizontal pattern of the 14 burrows, it was found that 9 burrows turned to the right, one to the left, one first to the right and then to the left, and 3 first left and then right. Of 12 burrows shown by Hallinan (1923), 6 turned to the right, 3 to the left, 2 right and then left, one left and then right. Both studies showed a predominance of burrows which were dug to the right.

Burrow Proportions. Hallinan (1923) reported the width of the burrow about twice that of the height. From 54 measurements in this study, the height/width ratio of the burrow entrance was 0.51. Two feet down the burrow, the same ratio was 0.54. The burrow entrance had a somewhat larger diameter resulting from rain erosion and lateral movements of the tortoise. The width of these 54 burrow entrances was 1.14 times larger than the burrow width at two feet. The height of the entrance was 1.08 times larger than that at two feet.

Fourteen measurements of occupied burrows, two feet from the entrance, averaged 7 inches for width and 3.5 inches for height. The tortoises taken from these burrows averaged 5.5 inches (greatest width) and 3.0 inches (greatest depth). Thus, the lateral excess space between the tortoise and its burrow (1.5 inches) is three times that of the height (0.5 inches).

Burrow Direction. Hallinan (1923) mentioned that the burrows enter the ground from all points of the compass. Present data agree, as 12 burrows faced predominately northward, 6 eastward, 7 southward, and 14 westward. A chi-square analysis of these data did not reach significance at the 5 per cent level of confidence and thereby suggests no directional preference by gopher tortoises.

Exposed Burrow Soil. A two dimensional surface measurement (greatest length parallel to burrow axis; greatest width at right angles to burrow axis) was recorded for the exposed subsoil fronting 24 burrows. In 1923 Hallinan reported that proportionately more sand was found at the entrance of burrows of smaller tortoises than at the entrance of larger ones. Contrary to Hallinan's findings, the present study showed the exposed soil to be strongly correlated with burrow size. Exposed soil measurements of width and length were significantly correlated with burrow width ($r = .84$, $P < 0.01$; $r = .77$, $P < 0.01$, respectively). A significant correlation was found between the exposed soil width and the length of burrows ($r = .60$, $P < 0.01$).

Vegetation. In general, the gopher tortoise seems to dig the burrow entrance in an area relatively clear from large vegetation. In the three habitats studied, no burrow entrance was found which had been dug closely adjacent to a heavy shrub or tree. Of 24 burrows examined in the Lakeland soil habitat, only 8 had trees within a 10 foot radius of the burrow entrance. These trees were small turkey oaks or longleaf pines with a diameter of 1-3 inches. Various herbs, primarily wire grass (*Aristida stricta*), grow from the exposed subsoil and are more heavily concentrated at the periphery. Many burrows have from 1 to 3 well-used trails, leading from the mouth of the burrow, which are free of vegetation.

Discussion

The lateral curvature of burrows is stated by a number of writers (Hubbard, 1893; Hallinan, 1923; Pope, 1939, Young and Goff, 1939) to be due to obstructions such as roots, rocks, hard materials, or other impeding objects. Each of the 14 burrows excavated in this study exhibited curvature. Yet, no roots nor hard materials which might have stimulated an animal to alter its course were encountered. Since the major portion of the burrow curvature continues at a depth beneath that where roots are normally found, the obstruction hypothesis is further questionable. A further evidence for burrow curvature as a function of digging behavior is that the curves are gradual and smoothly contoured rather than being markedly acute turns. From these observations one might surmise right or left footedness in the majority of individuals.

In all excavated burrows, the floor at the lower terminus was found covered with a fecal deposition of herbage that varied in quantity up to several inches in thickness. Since no fecal deposits were found along the floor of the burrow, the terminal accumulation would indicate that the animal spends the majority of its time at this point while in the burrow. This is in agreement with the conclusions of both Hubbard (1893) and Hallinan (1923), who suggest that the tortoise remains at the bottom of the burrow. In 13 cases where tortoises were retrieved, they were found at the bottom of the burrow, head downward. Prior to the excavation of 5 burrows, hose measurements were made of the burrow length. In each case it was found that the tortoise was at the bottom of the burrow.

One interesting find in this study, the first published record of its kind, was a double burrow occupied by a female gopher tortoise (Table 1, No. 7). The burrow entrance was single and quite typical in proportion. At a depth of 18 inches, some 25 inches from the entrance, the single burrow bifurcated into two well-formed burrows. The left-hand burrow curved off rather sharply to the left and then gradually back to the right. It measured 126 inches in length and 65 inches in depth at the terminus. The right-hand burrow was considered a newer addition since the animal was found occupying it, and it measured ¼ inch larger in diameter proportions. Although somewhat shorter (106 inches in burrow length) the angle of declination was greater and the burrow terminus depth was 68 inches. A few feet past the point of divergence, the two burrows generally paralleled one another at a distance of approximately 5 feet apart. Both burrows curved gradually to the right and terminated at almost identical vertical depths.

SUMMARY

A comparative study was made of the burrow system of *Gopherus polyphemus* from the Lakeland, Lakewood, and St. Lucie soil types common to Florida. Measurement of burrow length in 51 cases varied from 6.3 to 47.5 feet and averaged 15.3 feet. Two statistical analyses indicated no significant differences for burrow length in the three soil types. Tortoise size, burrow width, and burrow height were found to be significantly correlated with burrow length. The angle of declination for 14 excavated burrows

averaged 29° and ranged between 17 and 39°. In 14 excavated burrows, vertical depth from the surface to the burrow terminus varied from 4.6 to 9.2 feet and averaged 6.5 feet. Vertical depth failed to show a significant correlation with burrow length, burrow width, or burrow height. All excavated burrows exhibited horizontal curvatures with a predominance of patterns turning toward the right. In 54 measurements, the height/width ratio of the burrow entrance was 0.51. Two feet down the burrow this ratio was 0.54. A chi-square analysis suggested no directional preference as to burrow entrance. Measurements of exposed soil fronting 24 burrows showed a significant correlation with burrow length, burrow width, and burrow height. Burrow curvature appears to be a function of digging behavior and not soil obstructions. A description of a double burrow was given.

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